

- Fig. 6. Vertical section of the shell, passing through the chamber excavated by the sponge, and two of the nacreous papillæ.  $\times 8$ .
- Fig. 7. One of the same papillæ,  $\times 30$ , showing spicules of the sponge in the centre.
- Fig. 8. The skeleton-spicules.  $\times 110$ .
- Fig. 9. The larger flesh-spicules.  $\times 350$ .
- Fig. 10. The smaller flesh-spicules.  $\times 400$ .
- Fig. 11. One of the raphides.
- Fig. 12. Part of dermal membrane?
- Fig. 13. Gemmule?  $\times 40$ .
- Figs. 14, 15. Dermal spicules of a species of *Discodermia*, included in the tissues of the sponge.  $\times 80$ .

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On some Hermaphrodite Genitalia of the Codfish (*Gadus morrhua*), with Remarks upon the Morphology and Phylogeny of the Vertebrate Reproductive System. By G. B. HOWES, F.L.S., F.Z.S., Assist. Professor of Zoology, Royal College of Science, London.

[Read 5th February, 1891.]

(PLATE XIV.)

I. CODFISH possessed of hermaphrodite genital glands have been known since the days of Leewenhoek (1688), Baster (1761), Yarrell (1845), Smith (1870), Max Weber (1884), and others have since recorded examples. The fullest description of such yet published is that of Max Weber alluded to\*, to be referred to later, and his excellent paper embodies a *résumé* of all that was known up to the time of writing, with full references to the works of authorities cited. I have lately received from one of my past pupils (Mr. Walter C. Chappel, of Sunderland) the genitalia figured on Plate XIV., and our President has afforded me opportunity of examining five specimens in the Museum of the Royal College of Surgeons, under his charge. My best thanks are due to these gentlemen for their kindness and liberality.

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II. I give below the total lengths of the ovaries of the

\* Nederl. Tijdschr. v. d. Dierkunde, Jhg. v. Af. 2, p. 21 (1884).

specimens examined by Prof. Max Weber and myself. In no case was either the length or condition of the fish whence the organs were obtained known; but, except for a fatty degeneration undergone by the testis in the example numbered III., the animals appear to have been, in every case, healthy and productive of normal sexual elements.

*Table of Measurements of observed cases, with remarks thereon.*

The roman numerals refer to the Catalogue of the Royal College of Surgeons Museum.

	Total length in Centimetres.		
	Left ovary.	Right ovary.	
I. Max Weber, <i>loc. cit.</i> p. 23.	17·5	16·5	Testis present at posterior end of each ovary; confluence established on each side, by means of a short duct entering posterior pointed extremity of ovary.
II. Chappel (Pl. XIV. figs. 1, 2).	12	16	Testis present on right side only; confluence as with I.
III. 454 C .....	17	13	Testis (in bulk as large as the two ovaries together) on left side only; confluence over a wide area of the ventral postero-external border. Substance of testis largely fatty and degenerate; spermatozoa looked for but not observed.
IV. 446 .....	19	20·5	Testis on middle left side; confluence established over a wide area of postero-external border. Motile spermatozoa abundant.
V. 447 .....	12	12	Testis on right side; confluence as for I., II., by well-defined duct.
VI. 448 .....	12	12	Testis on right side; confluence established by a short duct, at anterior extremity of ovary.
VII. 449 .....	10·5.	10·0	Testis on right side; confluence established with anterior extremity of ovary as for VI.

In all six specimens which I have examined, both ovary and testis bore the normal characters and appearance; and in Mr. Chappel's example, which reached me fresh and unpreserved, the colour and general relationships of the organs were in every respect normal, and identical with those described by Max Weber (*l. c.* p. 24). Indeed, except for an important difference in the contents of the two (*cf. infra*, p. 542), and for the presence of a remnant of the genital duct, his detailed description might serve for the right half of my own specimen. The general characters of the several specimens enumerated differ most conspicuously in respect to the degree of backward prolongation of the ovaries beyond their point of union. In this, however, as in the inequality in length of the ovaries of opposite sides, there is nothing which changes consequent upon extrusion of the ova, together with the ordinary limits of individual variation, will not explain. And, moreover, the facts above tabulated clearly indicate that, in the Cod, the differentiation of a testis on the one or other side does not lead up to a corresponding reduction of the ovary. Rather the contrary (*cf. fig. 1*).

The genital organs of the Codfish are so well known, and Max Weber's description cited is so complete, that it is only necessary here to dwell upon certain special details of the specimens alluded to above. Firstly, as to the duct connecting the ovary and testis. Max Weber alludes to it (*l. c.* p. 24) as the "vas deferens—really a tube," &c.; he figures (pl. iii. fig. 2) a style passed into it, but tells us nothing of its orifice of communication with the ovary. In his drawing it is represented as skirting the inner two-thirds of the attached border of the testis; in my specimen (*d.t.*, fig. 1) it was much shorter, and the testicular substance was set upon it in the manner of a rosette. On laying open the duct I found it to be a spacious tube (*d.t.*, fig. 2), honeycombed in the manner of that of the normal male, over its upper and inner areas. Its lower moiety was longitudinally subdivided by a kind of septum (*v'*), which shut off a small orifice placing it postero-externally in communication with the interior of the ovary. There arose from the postero-internal wall of the ovarian capsule a stout membranous fold (*v''*), which projected inwards and passed, for a distance of 1 centim., towards the orifice of communication with the testis-duct; on nearing that it expanded to form a well-marked valve-like structure. It would thus appear that not only was there present a duct competent to

transport spermatozoa, but that a complicated apparatus existed in connexion with the same.

Spermatozoa were found in the testes of similar specimens examined by Weber and Halbertsma (*cf.* Weber, *l. c.* pp. 26, 27). Dr. Weber says of his specimen that (p. 24) the contents were of the nature of sperm mother-cells and spermatozoa "still united into bundles with their heads and tails in apposition," and that neither the male nor the female elements were as yet ripe. Mr. Chappel's specimen reached me, as already stated, while quite fresh. The remains of its duct of communication with the exterior (*d.g'*, fig. 1) were found to contain mobile spermatozoa; and, on careful examination, I was able not only to obtain these from the so-called vas deferens, but from the interior of the ovary also. Max Weber and others have surmised that the spermatozoa must, in such cases, ripen and pass out through the ovary; and my own observation proves this to have been realized. No one has yet detected the passage of ripe ova to the exterior in an hermaphrodite Codfish; and, in strictness, the declaration of a complete and functional hermaphroditism for this animal cannot be valid until such passage shall have been observed. In view, however, of the condition of the ovaries, and of the near approach towards maturation of their contents in my own specimen and in those of previous observers, there can be no reasonable doubt that we have to deal with true hermaphrodites, capable of producing both ova and spermatozoa.

Hermaphroditism among Teleostean fishes is well known. Aristotle knew *Serranus* to be hermaphrodite; and the recent researches of Syrski and Brock\* and others† have placed it beyond doubt that the hermaphrodite species of that fish are regularly self-fertilizing. Among the Teleostei generally the hermaphroditic condition is known for 16 genera and 19 species at fewest. In three of the former (*Centrolophus*, *Ophidium*, *Smaris*) the conditions remain doubtful, aggregations of ova having been found in the testes. The hermaphroditic condition has been recorded among the *Clupeidæ*, *Cyprinoidei*, *Esocidæ*, *Gadoidei*, *Labroidei*, *Percoidei*, *Pleuronectidæ*, *Scombroidei*, *Squamipinnes*, and *Sparoidei*—that is to say, among typical and wide-spread families of four of the six great orders now custom-

\* Morphol. Jahrb. Bd. iv. 1878, pp. 567 *et seq.*

† *Cf.* Brock, and Max Weber, *loc. cit.*



arily conceded, one or two others remaining doubtful\*. An hermaphroditic condition of the genital glands has been claimed for isolated members of other classes of Vertebrates. It is well known to occasionally manifest itself in the Amniota†; it is stated to be the constant condition for a solitary Batrachian; Pallas and Benecke have recorded it for *Acipenser*‡, and Semper for the Selachii§. Again, Langerhans has detected the tails of spermatozoa among young ovarian ova of *Amphioxus*||; and Cunningham¶ and Nansen\*\* have described what must be admitted to be, at least, a modified form of hermaphroditism in the Myxinoids.

Collation of the literature of this subject brings into prominence two striking facts, viz. :—*a.* That the frequency of occurrence of hermaphrodite genital glands in the Teleostei is common and widespread, as compared with other orders and suborders of Vertebrata; *β.* that whereas in the last-named (setting aside the Marsipobrauchii, in which the conditions are somewhat special, and the Bidder's organ of the Anura, as to the real nature of which we are still in doubt ††) the dominant condition is that of replacement of one of the two testes in an ovary, or *vice versá*, in the Teleostei it is that of the differentiation of the same gland into organically continuous ovary and testis. Notwithstanding the considerable attention which this subject has received, these facts have never before been sufficiently emphasized; and it remains now to follow them to their logical issue, and to enquire whether they may not have a deep significance. What, briefly, is the meaning of the repeated reversion of the genital gland to an organically continuous hermaphroditic type, which well nigh characterizes the Teleostei among Vertebrates?

Max Weber has proposed to distinguish between what he terms "true hermaphroditism" (such, for example, as that exemplified in the Codfish figured by him, in which testis and

\* For detailed list see Max Weber, *loc. cit.* pp. 36, 37.

† Cf. Sir James Simpson's article "Hermaphroditism," in Todd's 'Encyclopd. of Anat. and Phys.' vol. ii. p. 684.

‡ Cf. Max Weber, *loc. cit.* pp. 37–40.

§ Cf. Van Wijhe, *Archiv f. mikr. Anat. Bd.* xxxiii. p. 504 (1889).

|| *Ibid.* Bd. xii. 1876, p. 326.

¶ *Journ. Micr. Sci. n. s.* vol. xxvii. p. 49 (1887).

\*\* Aarsber. *Bergens Mus.* 1887, op. vii.

†† Cf. Knappe, *Morph. Jahrb.* Bd. i. p. 489 (1886).

ovary are continuous on either side and debouch on to the exterior), and those cases in which (*loc. cit.* p. 29), where the sexes are ordinarily distinct, individuals occasionally present themselves with testis and ovary on opposite sides. He would regard the latter as "pathological"; Brock has, however, objected to this distinction\*, upon what appear to me good grounds. It would be surely preferable to retain the term "pathological" for exclusively morbid and diseased conditions; and the well-established fact that the same blastema gives rise, by diverse modification, to both ova and spermatozoa, justifies us in regarding the various conditions of the adults last alluded to as degrees of abnormality † and nothing else.

The belief that the ancestors of the Chordata were hermaphrodite, for which Hæckel and others have specially contended, is daily gaining ground ‡. So frequent is the occurrence, and so marked are the physiological variations of the hermaphroditic condition of the genital glands among Teleostean fishes, that Syrski and Brock have been enabled to classify the same in accordance as the species are invariably § or only occasionally hermaphrodite, or as they are (*Serranus*) or are not (*Chrysophrys*) self-fertilizing. Leewenhoek, in 1688, adduced good reason to suppose that in the hermaphrodite Codfish which he examined the genital products ripened alternately, and that the animal functioned first as a male. In the specimen which I here figure this—the characteristic feature of "successive hermaphroditism"—had been realized (*cf. ante*, p. 542). Brock has shown that in *Chrysophrys auratus* the male and female genital products ripen alternately. Cunningham, in 1887, recorded (*loc. cit.*) the presence of both ova and spermatoblasts in the genital glands of the young Hag (*Myxine glutinosa*); and Nansen (*loc. cit.*), working at the same facts at the same time, has shown this animal to be in reality a protandric hermaphrodite, producing mature spermatozoa during its earlier existence, mature ova later in life. Apart from the fact that this Myxinoid, lowest of the low among living Vertebrata, has been thus shown to be regularly

\* Zeitschr. f. wiss. Zool. Bd. xlv. p. 373 (1886). *Cf.* Max Weber, Tijdschr. d. Ned. Dierkund. Vereen. ser. ii. D. i. p. 128 (1885-87).

† And that only as compared with the now predominant unisexual type.

‡ *Cf.* Van Wijhe, *loc. cit.* p. 504.

§ *Serranus cabrilla*, *hepatus*, *scriba*; *Chrysophrys auratus*, *Pagellus normyrus* (?). For detailed list see Max Weber, *Tijdschr. cit.* 1884, pp. 36-37.

hermaphrodite, the facts above cited are sufficient to suggest that the hermaphroditic condition, so marked among the Teleostei, may be reversional to, if not realistic of, that which must have been the ancestral condition for the Chordata\*. And if, as seems to me most reasonable, the unicyclic maturation of the ovotestis of the Hag is an abbreviated and specialized equivalent of the multicyclic one of the hermaphrodite Teleosteans, the question arises whether, in view of this, the bony fishes may not have retained a more primitive condition of the genital glands than have the other Gnathostomata †. On this supposition, their frequent reversion to the condition of hermaphroditism becomes at once intelligible, and, indeed, is that which might be expected.

Brock has shown ‡ that the reproductive apparatus of the Stylommatophorous Pulmonata is laid down upon the female plan, and that the later differentiation of the male parts is sometimes never effected. He seeks to apply this principle to the hermaphrodite Teleostei (*loc. cit.* p. 374); but, from examination of such of the latter as I have been able to obtain, I am strongly of opinion that further investigation will prove him to have been mistaken.

\* Laulanié has attempted to distinguish between successive phases of sexual neutrality, hermaphroditism, and unisexuality, in the ontogenetic development of the genital glands of the Amniota. He institutes comparisons with what he believes to have been the phylogenetic evolution of the organs named, and builds up an argument for primitive hermaphroditism (*Comp. Rend. t. ci.* pp. 393-395, 1885, & *Bull. Soc. Toulouse, t. xx.* pp. 13-16). Unfortunately, his observations are insufficient and of too incomplete a nature to justify the full acceptance of his statements.

† Experimental researches of the last six years have considerably modified the old belief that access to the sea is indispensable for the maturation of the genital glands of the Salmones. Not only have fish been found in the Parr stage with functional testes, but Day and Maitland have succeeded in rearing young from the eggs of 32 months' land-locked Parr of *Salmo salar* (*Trans. Linn. Soc. Lond., Zool. ser. 2, vol. ii.* 1885, p. 447 [*cf.* also Day's 'British and Irish Salmonidæ,' pp. 101 *et seqq.*]). In view of the above considerations, the probability that the earlier maturation of the genital gland of the male Salmonoid may be the expression of an ingrained tendency towards regular hermaphroditism must not be overlooked; and I would suggest the same interpretation of the recent discovery by Holt, that in the Mackerel the male organ would appear to be the first to mature (*Trans. R. Dublin Soc. vol. iv. ser. 2, p. 437, 1891*).

‡ *Zeitschr. f. wiss. Zool. Bd. xlv.* p. 374 (1886).

It is interesting, in view of this and in its possible bearing upon the ancestry of the Chordata, to recall the fact \* that the *Tunicata*, unlike the higher hermaphroditic Chordata, are mostly protogynous.

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III. That the genital ducts of adult Teleosteans, when present, are invariably continuous either with the membranes which suspend the genital glands or (most modified term) with those which invest them, is well known. They are frequently paired, becoming median and unpaired only when the glands are, as in the female Cod, united and saccular. The steps in the realization of this continuity have been worked out by Jungersen † and others. The urino-genital organs of the Teleostei differ collectively from those of all other Vertebrates, with the exception of the *Ganoidei* and *Marsipobranchii*, in the absence of undoubted vestiges of the genital ducts of the opposite sex.

Balfour, in dealing, at the end of his career, with the development of the urino-genital system of the Vertebrata generally, laid it down as his final conclusion ‡ that the ducts of the Teleostei are most probably “in both sexes . . . modified Müllerian ducts” (*cf.* *l. c.* p. 606); and he further pointed out that while analogy would suggest that they might (p. 580) “correspond with the Müllerian ducts of Elasmobranchii,” &c., on this point there was “no positive embryological evidence.” Balfour was contending for his belief in the homology of the “Müllerian ducts” throughout the Vertebrata, as tubes formed in relation to the head kidney and to a splitting of the segmental ducts §. The tendency of post-Balfourian investigation into the morphology of the vertebrate urino-genital system has been towards the overthrow of this conception; and, indeed, with the recent discoveries of Van Wijhe ||, Marshall and Bles ¶, and others named on the next page, the Elasmobranchii occupy a well nigh isolated position as the only great group of Vertebrata for which it has not been either

\* *Cf.* Herdman in ‘Challenger’ Reports, vol. xiv. Tunicata, p. 23.

† *Loc. cit.* p. 179.

‡ *Comp. Embryology*, vol. ii. p. 605.

§ *Cf.* Sedgwick, *Quart. Journ. Micr. Sci.* n. s. vol. xxi. p. 468 (1881).

|| *Archiv f. mikr. Anat. Bd.* xxxiii. p. 461 (1889).

¶ *Studies Biol. Lab. Owens Coll. Manchester*, vol. ii. p. 185 (1890).



overthrown or, at least, challenged on tolerable grounds. Balfour and Sedgwick were the first to clearly show that the Müllerian duct of the Amniota might be (chick) a compound structure, for the first part of its course split off as a solid and backwardly-extending rod "from the outer or ventral wall of the Wolffian duct." Concerning the "posterior part of its course," Balfour wrote that "its growing point lies in a bay formed by the outer walls of the Wolffian duct, but does not become definitely attached to that duct. It seems, however, possible that, although not actually split off from the walls of the Wolffian duct, it may grow backwards from cells derived from that" (*loc. cit.* p. 592)\*.

Conspicuous among the post-Balfourian researches afore alluded to are those of Milhálkovics †, Jungersen ‡, Wiederheim §, and others, which have revealed the fact that the Müllerian duct of the Amniota is formed, mainly if not entirely, as a derivative of the peritoneum, wholly independent of the Wolffian duct, arising far forwards and gradually extending back. Jungersen's extensive inquiry was especially directed towards the Teleostei. He found that the genital duct of the female arises as a peritoneal derivative, formed late—that is, subsequently to the differentiation of the genital gland, with the investment of which it becomes subsequently connected ||. Relying upon his discovery of this independent origin he argues, from analogy to the independent origin of the Müllerian ducts of the Amphibia and Amniota, in favour of an homology between the two, and shows ¶ that the genital duct of the female Teleostean may be looked upon as either partially or entirely homologous with the Müllerian duct proper, in accordance with different views which he formulates.

Jungersen has observed that whereas in the females the genital duct arises independently of the gland, in the males the two appear to be from the first continuous; and he urges this as a fundamental distinction between the sexes. The leading variations in the structure and relationships of the fully

\* *Cf.* also Quart. Journ. Micr. Sci. vol. xiv. n. s. p. 9 (1879).

† Month. Internat. Journ. of Anat. & Hist. vol. ii. p. 284 (1885).

‡ Arbeit. a. d. Zool. Zoot. Institut. Würzburg, Bd. ix. p. 89 (1889).

§ Archiv f. mikr. Anat. Bd. xxxvi. p. 410 (1890).

|| *Loc. cit.* pp. 179 *et seqq.*

¶ *Loc. cit.* pp. 192–200.



formed ducts of the males and of those females in which they are completely closed are well known to affect the opposite sexes indifferently; these weighty facts of anatomy bear out Balfour's deduction (*cf. infra*) that the ducts are homologous in both sexes, and completely override the force of Jungersen's discovery. By a Müllerian duct we understand one invariably arising far forwards, either in relation or immediate proximity to the head kidney, when such exists, and becoming for the most part completed by a process of backward extension. The researches of Jungersen show clearly that the one distinguishing feature of the Teleostean genital ducts is their restriction, alike in origin and relationship, to the posterior genital region; and, whatever may be said for their supposed homology in the two sexes, this fact is, to my mind, fatal to the supposition that that of the females represents a Müllerian duct as ordinarily understood.

Jungersen's Teleostean's genital duct arises, like Balfour and Sedgwick's posterior segment of the Chick's Müllerian duct, late, and in juxtaposition to the base of the Wolffian or segmental duct. The Müllerian duct of the *Anura* is asserted by Hoffmann\* to arise for the most part as a backwardly extending derivative of the peritoneal epithelium. Fürbringer describes the Müllerian duct of the Urodela † as formed (*Salamandra*) of an anterior segment derivative of a thickened and backwardly extending portion of the peritoneal epithelium, and a posterior one arising as a solid product of the wall of the pro-renal duct ‡. These facts not only strengthen the conclusion that the female genital duct of the Amniota and Amphibia is in all probability a compound structure, but, in view of the isolated position of the Elasmobranchii already referred to on p. 546, they suggest that it may not be serially homologous for the three groups. Upon this possibility future investigation must decide. The facts, taken in conjunction with those to which I have herein drawn attention, point, I believe, most markedly, to another and simpler conclusion, viz.: that the genital ducts of the Teleostei are in both sexes distinct from those of Elasmobranchs, Amphibians, and Amniota, and that

\* Zeitschr. f. wiss. Zool. Bd. xlv. p. 594 (1886) (*cf.* Marshall & Bles, *op. cit.* pp. 142-143).

† Morph. Jahrb. Bd. iv. p. 31 (1878).

‡ *Cf.* v. Wijhe & Jungersen, *op. cit.*

they are (as has been already suggested for that of the females by McLeod \*, Brock †, and Max Weber ‡) independent structures *sui generis*. At the same time I consider it not improbable, from the facts afore cited, that the posterior moiety of the Müllerian duct of at least the Amphibia and Amniota may be the vestige of that which has survived in the Teleostei, and that its anterior moiety is a more recent structure which has replaced the latter in time.

Brock inclines to the belief that the hermaphroditic condition of the genital glands has been independently evolved within the vertebrate phylum. I venture to think that had the discoveries of Cunningham and Nansen (*ante*, p. 543) preceded Brock's, he would have arrived at a different conclusion. These and the constantly hermaphroditic habit of the Tunicata appear to me irreconcilable with his supposition, to say nothing of the facts which I have emphasized in dealing with the Teleostei (*ante*, p. 545) and of Langerhans' discovery of spermatozoa in the ovary of *Amphioxus*. While I entirely disagree with Brock's second proposition, I fully acquiesce in his first, and with Beard § regard both Teleostei and Ganoids as at all stages wholly destitute of Müllerian ducts. The genital duct of these fishes is, like the gland which it serves, hermaphroditic in tendency; and, in view of the facts and considerations with which I have dealt, I consider that their reproductive system may, most satisfactorily and with some foundation, be regarded as the most generally primitive among living Gnathostomata.

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IV. Huxley, in 1883, drew attention || to the lack of appreciation which has attended Rathke's observations on the genital ducts of fishes; and he proceeded to describe the parts now in question in the female Smelt (*Osmerus eperlanus*), showing them to be readily harmonizable with those of the other Salmonoidei and Ganoids, *Lepidosteus* excepted. The Smelt's ovary is, as

\* Arch. d. Biol. vol. ii. p. 497 (1881).

† Zeitschr. wiss. Zool. Bd. xlv. p. 375 (1886).

‡ Morph. Jahrb. Bd. xii. p. 396 (1887).

§ Anat. Anz. 1890, p. 158.

|| Proc. Zool. Soc. Lond. 1883, p. 132.

Huxley shows, lamelligerous and freely pendent, and reflected ventro-externally; while its duct is incompletely tubular and directly continuous with the mesovarium. The ducts of opposite sides pass back, converging as they do so, to communicate with the exterior through the mediation of a shallow sac opening by a porus genitalis disposed immediately behind the anus. Huxley has pointed out, among other things, that this pore can have nothing to do with the pori abdominales of Ganoids and Elasmobranchs; and, were not his reasoning sufficient, the later discovery by Max Weber\* of the general co-existence of the two in Salmonoids disposes of future misunderstanding on this point.

Balfour and Parker have shown (as Huxley points out †) that the oviduct of *Lepidosteus* passes through an Osmeroid stage in its development; and the recent researches of Jungersen have proved ‡, on appeal to embryology, that the oviduct of *Osmerus* is, as Huxley supposed, homologous with that of all other bony fishes and Ganoids.

It is now known that whereas in the majority of Teleostei and in *Lepidosteus* the ovary is a closed sac, lodging a central cavity continuous with the lumen of its duct, in the *Osmeroidei* and in the remaining Ganoids the former is a folded plate and the latter a more or less incomplete tube with a wide ostium; while in the *Salmones*, *Murænidæ*, and *Cobitis* §, as in the *Galaxiidæ*, *Notopteridæ*, and *Hyodon* ||, the "oviduct" is either insignificant or absent.

Jungersen's researches place it beyond doubt that the genital pores of those Teleostei devoid of genital ducts are one and the same with the ostia of the latter when present. Relying upon his discovery that the genital glands are well differentiated before traces of their ducts ever appear, he has concluded (*loc. cit.* p. 183) that the ductless condition must have been the more primitive one. Against this must be set:—i., the invariable

\* *Morph. Jahrb.* Bd. xii. p. 366 (1887).

† *Loc. cit.* p. 136.

‡ *Loc. cit.* pp. 181 & 192.

§ Rathke, "Ueb. d. Darmkanal u. d. Zeugungsorgane d. Fische," *Schrift. d. naturf. Gesellsch. z. Danzig*, H. iii. Bd. 24 (1824).

|| *Cf.* Günther, 'Introd. to Study of Fishes,' p. 158; and Jungersen, *loc. cit.* pp. 1 & 182-3.

presence of the ducts in the male Teleostean; ii., the undoubted fact that the general organization of *Osmerus* is of a much lower type than that of either *Salmo* or *Cobitis*, not to say than that of the other ductless genera named.

On the whole, I am inclined to acquiesce in the view of Rathke \*, Huxley †, and Balfour ‡, and to regard the Salmonoid-Murænoïd type as the expression of a loss of the ducts; but I look upon the Osmeroid type as the lowest term in the series, and consider the more typically Teleostean condition (ex. *Gadus*) on the one hand and the Salmonoid-Murænoïd one on the other, as having resulted from divergent modification of the former along opposite lines. Huxley has proposed § to term the closed condition (ex. *Gadus*) the *Cystoarian*, and that of the Smelt the *Elasmoarian*, and for the ductless type the designation *Gymnoarian* may perhaps suffice. I would point out, in support of my conclusion, that *Argentina*, whose genital glands have been shown by Max Weber || to be in a less specialized condition than those of *Osmerus*, has well-developed ducts; and that the researches of McLeod, Balfour and Parker, and Brock have shown the cystoarian type to pass through an elasmoarian stage. Further, by way of guarding against future confusion between the simple so-called "oviduct" of the Teleostei and Ganoids and the more complex Müllerian oviduct of other Vertebrata, which are in all probability non-homologous, the former might be termed the *ovary-duct*.

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V. To turn, in conclusion, to the *Marsipobranchii*. The genital organs of these fishes discharge their products through a couple of perforations in the side walls of the so-called urinary or urino-genital cloaca. Müller long ago described in relation to these so-called "abdominal pores" membranous tubes; and Vogt and Pappenheim have described in relation to each a short

\* *Loc. cit.* pp. 124-125.

† Proc. Zool. Soc. Lond. 1883, p. 137.

‡ Comp. Emb. vol. ii. p. 580.

§ Lectures, 1884. For permission to embody the terms employed in this paragraph, the author acknowledges his deep indebtedness to his honoured master.

|| Morph. Jahrb. Bd. xii. p. 395.

canal. Unfortunately, subsequent investigation has not borne out these statements\*.

The urinary and genital pores of the Teleostei open upon the exterior, as is well known, either independently or through the mediation of a common urino-genital sinus, and the two orifices may, in some of the first-named cases, be embraced by a tegumental fold suggestive of a vestige of the sinus named. In view of the researches, more especially of Huxley, Balfour, and Jungersen, already recapitulated, it can hardly be doubted that the genitalia of the Ganoids and Teleostei conform to a common type, variable in nothing more than degree of inter-communication between the genital and urinary ducts. That the cystoarian condition, as exemplified by *Lepidosteus* on the one hand and the majority of living Teleostei on the other, would appear to have resulted from a parallelism of modification is, I think, sufficiently clear.

I have shown reason (*ante*, p. 548) for adhering to Balfour's belief that the generative ducts are homologous in both sexes of Teleostei; and if it be true of them it must be so of the Ganoidei also. If this is, as I believe, sound, it is fair to assume, in consideration of the facts of anatomy and development recapitulated in the foregoing pages, that there must have existed a piscine type in which the male apparatus was in the elasmobranch condition—in which, that is to say, the so-called "vas deferens" was an incomplete tube with a wide ostium. No ichthyologist will need to be reminded that this is precisely the condition of the parts in the Sturiones, except that no one has yet succeeded in proving that the duct transmits the spermatozoa †. In the Sturiones the genital glands extend throughout the whole length of the post-pericardiac cœlom; and Max Weber's discoveries among the Salmonoids ‡ show that in the higher Osteichthyes we have to deal with an abbreviation of this condition. In fact, the Sturgeons present us with exactly that which my hypothesis demands. Balfour and Parker have concluded § that "the most primitive

\* *Cf.* Ewart, *Journ. Anat. & Phys.* vol. x. p. 488 (1876).

† *Cf.* Hyrtl, *Denkschr. Akad. Wien*, 1855, pp. 1-5; Johannes Müller (*Hyrtl cit.*), and Jungersen, *loc. cit.* pp. 185-187.

‡ And especially *Argentina*, see *Morph. Jahrb.* Bd. xii. p. 395.

§ *Phil. Trans.* 1882, part ii. p. 423.



type of Ganoid genital ducts is found in the Chondrostei." In consideration of the facts alluded to on p. 551, I would go further and suggest that the general plan of structure of the Chondrostean's genitalia is the most primitive of that of all living Gnathostomata, and that it most nearly realizes that type from which the latter originally diverged.

The Salmones are among those Teleostei in which the ovary-ducts are absent, and the urino-genital sinus in them (Pl. XIV. figs. 3 & 4, s.) assumes the form of a well-defined sac which receives the ureters posteriorly (*bl.*"') and is in the female perforated laterally by the pori genitales (cf. *br.*"' of fig. 3). Comparison of the male (fig. 4) shows these pores to correspond in position with the ostia of the genital ducts (*d.g.*"'). These facts have been long ago described and figured by Carus and Otto\*. Comparison of those Salmonoids possessed of both abdominal pores and oviducal slits (figured by Carus and Otto and by Max Weber) with the Marsipobranchs, seems to me little short of fatal to the view entertained by Balfour†, Bridge‡, and others, that the pori genitales of the latter represent the pori abdominales of Elasmobranchs, Ganoids, and Teleosteans. If they do, in entering into relationship with the walls of the urinary sinus they must have undergone a translocation for which there is no suggestion of a parallel elsewhere. On the other hand, comparison of both sexes of the Marsipobranchs with those of the Salmones points, much more naturally, towards a direct homology between the parts in question. Deepen the sac of the female Salmon (fig. 3), even to the extent of that of the male (fig. 4), or shorten that of the Marsipobranch, and it would be difficult to distinguish between the two types. And if, as Scott asserts §,

\* Erläuterungstafeln z. vergleichend. Anat., Heft. v. Leipzig, 1840, pp. 8-9, pl. iv. fig. 5 & pl. v. fig. 3.

† Journ. Anat. & Phys. vol. x. pp. 34-35 (1876).

‡ *Ibid.* vol. xiv. p. 86 (1879).

§ Morph. Jahrb. Bd. vii. p. 167 (1882). Cf. Shipley, Quart. Journ. Micr. Sci. n. s. vol. xxvii. p. 352 (1887). Compare also the account of the development of the urinary ducts of the Teleostei, given by McIntosh and Prince, Trans. R. Soc. Edinb. vol. xxv. part iii. p. 785 (1890). Most interesting and suggestive in view of Scott's declaration is the recent discovery by Liszt (*Zeitschr. wiss. Zool.* Bd. xlv. p. 595, and *Anat. Anz.* 1890, p. 640) that in *Crenilabrus pavo* the so-called urinary bladder of the embryo opens for a short time into the base of the alimentary canal.

the urino-genital sinus of the Marsipobranch is a hypoblastic sac, split off from the enteric tube, the difficulty of homologizing the perforations of its side walls with the cloacal pits of the other Pisces, which are epiblastic in origin, will be still further increased. With this the mind reverts to Rathke's original view\*, shared by Gegenbaur and others, that the Marsipobranchii should be included in the category of those fishes which have lost their genital ducts.

Inasmuch as their ducts are absent in both sexes, they may be said to be in a *gymnogonarial* condition, as distinguished from the gymnoarian Osteichthyes, in which the females only are ductless.

The chief obstacle in the way of accepting Rathke's view has undoubtedly been the failure of embryologists to find traces either of a splitting of the segmental duct or of parorchis and parovarium in the young of these fishes. If the view of the phylogeny of the Teleostean "ovary-duct" which I have sought to establish should remain valid, this objection will have been largely dispensed with; for, inasmuch as the Marsipobranchs, together with the *Salmones*, *Murænidae*, *Galaxiidae*, *Notopteridae*, *Hyodon*, and *Cobitis*, would appear to have lost not the Müllerian duct but the primitive and hermaphroditic "ovary-duct," the demand for vestiges of the former will be no longer a *sine quá non*.

Balfour has long ago pointed out † that "the condition of the urino-genital organs in Selachians is by no means the most primitive found amongst Vertebrates." Powerful arguments in favour of a belief in convergence of the living Marsipobranchii, Ganoidei, and Teleostei towards a common stock, unrepresented at the present day, have been lately put forward ‡ by Beard. Eddinger has shown the structure of the prosencephalon of the Batoidei to be more primitive than that of the Sharks, and I have been enabled to prove § that, with respect to its dorsal mesentery, the Torpedo *Hypnos subnigrum* is far more primitive than all other Plagiostomes. The latest palæontological researches of Cope|| and

\* *Loc. cit.* p. 123.

† Journ. Anat. & Phys. vol. x. p. 28 (1876).

‡ Anat. Anz. 1890, pp. 146 & 179.

§ Proc. Zool. Soc. Lond. 1890, p. 671.

|| Amer. Nat. vol. xxiv. p. 402 (1890).

Smith Woodward \* have forced them to conclude that both the living Elasmobranchs and Teleosteans are specialized members of their types; they look upon the two as equally ancient, and as connected with some lower types of greater antiquity, now wholly extinct. Putting all together, I accept their conclusions, except so far as they involve the so-called archipterygial type of fin; and that the facts and considerations dealt with in this paper tend in the same direction will, I trust, be obvious from the context.

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VI. *Lepidosteus* is well known to be the only living cystoarian Ganoid. Balfour and Parker, when dealing with its reproductive organs, observed that its ovary and ovary-duct pass through an Osmeroid stage (*cf. ante*, p. 550). On having concluded † that the genital products of the male are transported by vasa efferentia through the mesonephros, they suggested that “the Teleostei must . . . have sprung from Ganoids in which the vasa efferentia had become aborted.” Jungersen has shown reason for doubting this observation (made only upon one specimen of 60 centim. in length) ‡; but even if it should hold good, I am of opinion that their suggestion by no means follows as a logical conclusion. For equally good arguments might be brought forward to show that *Lepidosteus*, instead of representing, as they would have us believe, a type transitional in these respects between Elasmobranchs and other Ganoids, might typify a culminating term in the Ganoid series as now represented; the “vasa efferentia,” as it were, first appearing instead of languishing. The position of Balfour and Parker assumes that the type of structure exemplified in the urino-genital system of the living Elasmobranchs is necessarily more primitive than that of the Ganoids and Teleosteans. All subsequently discovered facts of comparative embryology of the system named are in complete opposition to this; and it will, I trust, be admitted that the general structural features of *Lepidosteus* are most nearly in harmony with

\* British Mus. Cat. Fossil Fishes, vol. ii. pp. xi, xxi (1891).

† Phil. Trans. 1882, part ii. p. 424.

‡ *Loc. cit.* p. 188.

the views herein put forward (*cf.* p. 552). Indeed, the study of *Lepidosteus*, and of the facts just briefly alluded to, suggests—if it be granted that the Chordata were primitively hermaphrodite,—that the differentiation of the Wolffian and Müllerian ducts was associated with the first step towards unisexuality, and that the presence of remains of the one or other of these ducts in the opposite sexes of the Vertebrata in the form of a non-functional vestige is far from being an index of hermaphroditism, as has been frequently supposed.

My friend Prof. W. N. Parker has lately shown \* that in *Protopterus* Müllerian ducts are present in both sexes. He has further made the very important discovery † that in the male vasa efferentia are absent, the testis-duct being, like that of Osteichthyes, continuous with its gland—or, to state the facts otherwise, that epididymis and vas deferens are unrepresented. From my standpoint two most striking conclusions arise from this, viz. :—(α) that in the perfection of unisexuality the formation of the Müllerian duct must have preceded that of the vas deferens ; and (β) that the Dipnoi must have struck off from the parent stock during the interval in the differentiation of the two ‡.

The living Vertebrata, as classified by their urino-genital system, fall into two readily discernible series, viz. :—(α) the *Nephrochidic series*, embracing the Elasmobranchii, Amphibia, and Amniota, in which vasa efferentia are present and the excretory organ is an accessory to reproduction in the male ; (β) the *Euthorichidic series*, embracing the Ganoids, Teleostei, Marsipobranchii, and Dipnoi, in which vasa efferentia are unrepresented, and the Wolffian or segmental duct is exclusively renal in function. That the latter type must be looked upon as the more primitive is clear, from all recent discovery in the morphology of the

\* Berichte d. naturf. Gesellsch. Freiburg i. B., Bd. iv. Heft 3, p. 22 (1888).

† As yet unpublished. I here acknowledge my indebtedness to him for permission to mention his observation.

‡ It follows from this that whatever be the affinities of the Dipnoi, they can have nothing to do with living Ganoids. Indeed they appear to me to have left the Holocephalic branch of the Elasmobranch stock prior to the differentiation of the immediate ancestors of its living members. In this belief and in my views of the inter-relationships of the Ichthyopsida, I find myself in complete harmony with Beard (*cf.* Anat. Anz. 1890, p. 186).

§ εὐθύς, straight.

urino-genital system. The Dipnoi appear to occupy a partially central position in the collective series; and while the Marsipobranchii are undoubtedly referable to a much lower stock than all other living Chordata with the exception of *Amphioxus* and the Tunicata, their living representatives would appear to have suffered the loss of their genital ducts. The facts concerning them, as I have endeavoured to interpret them, point to an apterygial\* Chondrichthyan with hermaphrodite duct bearing genitalia as, to my mind, the most logically conceivable ancestor of the living Vertebrata.

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I claim for my hypothesis,—i., a not inconsiderable foundation in fact; ii., that it enables us to harmonize the facts of morphology of the genitalia of Vertebrates (and especially those of the *Osteichthyes* so long considered anomalous), at least as satisfactorily as any other yet postulated. It renders explicable the absence of vestiges of the ducts of the opposite sexes in the *Osteichthyes* and *Myxichthyes*, in that they would appear to have never been formed; and it furnishes at least a possible explanation of the constantly recurring reversion of the Teleostean genital glands to an hermaphroditic type.

#### EXPLANATION OF PLATE XIV.

- Fig. 1. Genital glands of an hermaphrodite Codfish (*Gadus morrhua*); with remains of genital duct, urocyt, and suspensory ligaments. Ventral aspect. One half natural size.
- Fig. 2. The same; head of right ovary with testis-duct, laid open to show their interior and details of communication. Natural size.
- Fig. 3. *Salmo salar*, ♀. Dissection to show the interior of the urino-genital sinus, and relations, to the same, of the urinary and genital orifices. After Carus and Otto (ref. see p. 553).
- Fig. 4. *Salmo salar*, ♂. Comparison dissection to fig. 3. After Carus and Otto.

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\* I would suggest this term to express the absence of paired fins, as distinguished from the apodal condition in which the pelvic members are alone wanting.



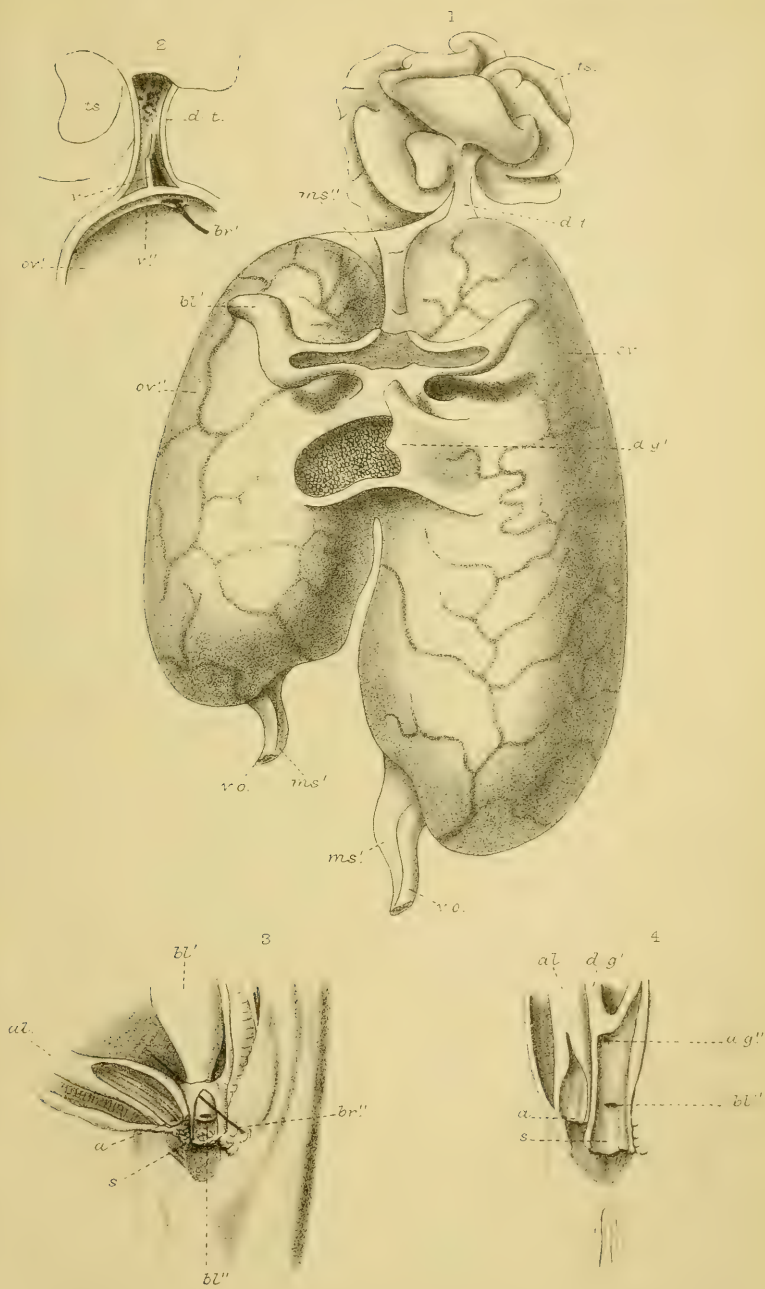
*Reference letters.*

<i>a.</i> Anus.	<i>d.t.</i> Testis-duct.
<i>al.</i> Intestine.	<i>m.s'</i> Suspensory ligament of ovary.
<i>bl'</i> Urocyst (so-called urinary bladder).	<i>m.s''.</i> Mesenteric fold.
<i>bl''.</i> Orifice of the same.	<i>ov'</i> Right ovary.
<i>br'</i> Bristle passed from interior of right ovary into testis-duct.	<i>ov''.</i> Left ovary.
<i>br''.</i> Bristle passed into porus genitalis of right side.	<i>ts.</i> Testis.
<i>d.g'</i> Genital duct.	<i>s.</i> Urino-genital sinus.
<i>d.g''.</i> Orifice of the same.	<i>v'</i> Longitudinal septum of testis-duct.
	<i>v''.</i> Valve-like fold at base of testis-duct.
	<i>v.o.</i> Ovarian vein.

A Revised Classification of the TUNICATA, with Definitions of the Orders, Suborders, Families, Subfamilies, and Genera, and Analytical Keys to the Species. By W. A. HERDMAN, D.Sc., F.L.S., Professor of Natural History in University College, Liverpool.

[Read 5th February, 1891.]

DURING the three years which have elapsed since the last part of the report upon the Tunicata collected during the 'Challenger' Expedition was written, I have had opportunities of examining, more or less in detail, many large collections of Tunicata from various parts of the world, including especially three important series of specimens from Australian seas which are now in my laboratory, viz.:—the collection of the Australian Museum, Sydney (from which I am drawing up a Museum Catalogue); a collection made by Mr. Bracebridge Wilson in the neighbourhood of Port Phillip, and sent to me for description by Prof. Baldwin Spencer; and, lastly, the collection made by Prof. Haddon in the Torres Straits. I have also been able to make a number of observations from the living animals on various parts of our own and the French coasts. Consequently I feel that I am in a position now to revise the classification put forward in the 'Challenger' Report, to deal with those few genera not included in that work and those described since 1888, and to



G.B.H. del ad nat.  
M.P. Parker lith.

West, Newman imp.

GENITALIA OF HERMAPHRODITE CODFISH.